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THE HABIT OF LEAF-OVIPOSITION AMONG THE PARASITIC HYMENOPTERA.[1]

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Entomologists have for some time been more or less familiar with the strange habit of leaf-oviposition in the parasitic dipterous family Tachinidæ. Twenty-nine years ago Dr. C. Sasaki of the Imperial University of Japan[2] made the interesting discovery that the so-called Ugi parasite of the silkworm (*Crossocosmia sericariæ* Corm.) deposits its eggs not within or upon its host, as was the habit of all other known parasites, but upon the leaves of the food plant of its host, *i. e.*, the mulberry tree. These eggs were minute and very numerous and were taken into the alimentary canal of the silkworm along with the mulberry leaves upon which it fed. Later, in 1908, Mr. O. H. Swezey[3] found the same curious habit to occur in the life-history of the Tachinid *Chætogædia monticola* Bigot, a parasite of various lepidopterous insects in the Hawaiian Islands. During the same year Mr. C. H. T. Townsend[4] of the U. S. Bureau of Entomology recorded this curious habit in the Tachinid *Blepharipa scutellata* R. D., introduced into New England from Europe as an aid to the suppression of the Gypsy Moth, and in *Pales pavida* Meigen, introduced for the same purpose. Mr. Townsend also mentioned several other species which he suspected to have the leaf-oviposition habit. Another curious deviation from the regular methods of reproduction Mr. Townsend found to occur in *Eupeleteria magnicornis* Zetterstedt, and *Zygobothria nidicola* Townsend, these flies depositing living maggots on the leaves upon

[1] Occasional Contributions from the Cal. State Insectary, No. 5.

[2] Sasaki, C., On the Life-history of *Ugimya sericaria* Rondani. Journ. Coll. Sci. Imp. Univ. Japan, Vol. I, pp. 1–39, 1887.

[3] Swezey, O. H., Observations of the Life-history of *Chatogædia monticola* Bigot. Proc. Hawaiian Ent. Soc., II, pp. 1–35, 1908.

[4] Townsend, C. H. T., A Record of Results from Rearings and Dissections of Tachinidæ. Bull. U. S. Dept. Agric., Bur. Ent., Tech. Ser., No. 12, pp. 93–118, 1908.

which the host feeds. The maggots attach themselves to the caterpillar host as it crawls over the food plant, and later bore their way into its interior. Recently Mr. J. L. King, of the Ohio Experiment Station, has given us an extremely interesting account of the same general habit, the subject of his studies being the Cyrtid *Pterodontia flavipes* Gray, a parasite of spiders.[1] Up to the present time, however, no such startling deviation from the normal has been observed in the parasitic Hymenoptera.

In 1909 and 1910 the writer, while engaged in the study of the hymenopterous parasites of the Gipsy and Browntail Moths at the laboratory of the U. S. Bureau of Entomology, Melrose Highlands, Mass., carried on an investigation of the life-history and habits of *Perilampus hyalinus*, a hyperparasite of the Fall Webworm. In brief the life-history of this chalcidoid parasite was found to be as follows: Nothing in regard to the egg-laying habits could be ascertained. The first stage larva, however, a very curious being, heavily armored with chitinous plates and provided with numerous curved hooks and spines, was found crawling about on the outside of the caterpillar. Later these first stage larvæ or planidia were found to bore their way into the body cavity of the caterpillar, there swimming about freely until the primary parasite larva, either hymenopterous or dipterous, was found, and into which they gained entrance. The Perilampus larva then remained quiescent until the primary parasite became full-fed and made its exit from the caterpillar to spin its cocoon or form its puparium. At the time of ecdysis the planidium found its way to the exterior of the host, after which it fed as an ectophagous parasite in the normal way. The egg-laying habit of this strange parasite has, however, remained a puzzle to entomologists, and at that time the writer made the following statement in regard to it:[2]

"There have been made, so far as published records go, at any rate, no observations upon the oviposition of members of the genus *Perilampus*. It is known, however, that oviposition does not occur in the normal way, or in the manner we are accustomed to regard as the normal method of oviposition among the parasitic Hymen-

[1] King, J. L., Observations on the Life-history of *Pterodontia flavipes* Gray (Diptera). Annals Ent. Soc. Am., Vol. IX, p. 309–321 (1916).

[2] Smith, Harry S., The Chalcidoid Genus Perilampus, and its Relation to the Problem of Parasite Introduction. Bull. U. S. Dept. Agric., Bur. Ent. Tech. Ser., No. 19, pp. 33–69, 1912.

optera, and for this reason speculations on what may actually occur are rather interesting.

"In the first place it is obvious from the facts recorded in the preceding pages that *Perilampus* does not oviposit directly in or upon its host. In the second place, it does not oviposit within the caterpillar of which its host is a primary parasite, which is equally obvious from the observations already made. That it places its eggs *upon* the young caterpillar is improbable, the adult *Perilampus* being too slow and clumsy to be capable of accomplishing this act with any degree of certainty.

"There are two plausible methods which *Perilampus* might adopt for the deposition of its eggs, and the writer is strongly inclined to the view that one of these methods is in part at least correct. As in the case of some of the parasitic beetles, it may deposit its eggs upon flower heads or upon leaves of plants not in the immediate vicinity of the caterpillar colony, the planidia hatching from these eggs being conveyed to the caterpillars by means of some intermediate carrier. In the Coleoptera cited above the carrier is frequently a parasitic bee upon which, by means of their claws, the triungulins attach themselves and are conveyed to the nest of their host. With *Perilampus*, should this method prove to be the one which really takes place, the intermediate carrier might be any of the primary parasites which attack *Hyphantria;* that is, the hymenopterous parasites *Limnerium* or *Apanteles*, or the Tachinid *Varichaeta*. The planidium seems more or less fitted for this sort of a life and is apparently analogous to the triungulin of the coleopterous parasites. The chitinous plates with which it is armored are especially serviceable in preventing injury of various kinds, and the mandibles and hooks and spines would serve it very well as a means of clinging to its conveyer. . . .

"The other method, which seems much more plausible, is that of oviposition upon the food plant *in the vicinity of a colony* of the caterpillars. This would do away with the necessity of an intermediate carrier, but would expose the delicate eggs to great danger unless they hatched immediately after deposition. . . .

"While the eggs of *Perilampus* have not been observed after deposition, those contained in the ovarian tubes, in one case ap-

parently mature, have been examined. They are of the usual elongate-oval shape, not stalked, and whitish in color."

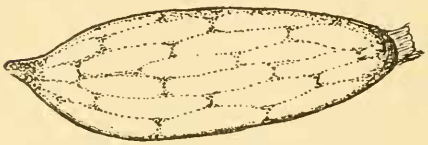

Fig. 1. Egg of *Perilampus chrysopæ* var., greatly enlarged. (Original.)

For seven years the writer has been looking for a chance to corroborate or disprove the theories advanced in the above statement, but the opportunity did not present itself until about two weeks ago. During the previous summer specimens of *Perilampus* were occasionally bred from *Chrysopa* cocoons. Recently the writer was successful in capturing several adult female *Perilampus*[1] of this species hovering about oleanders infested with *Aphis nerii* and fed upon by *Chrysopa*. The insects were then watched and were observed frequently to touch the tip of the abdomen to the leaf. On placing the leaf under the binocular microscope the minute transparent eggs of the *Perilampus* were seen, one end of the egg being slightly attached to the leaf. This observation proved the correctness of the original theory and established beyond doubt the habit of leaf-oviposition among the parasitic Hymenoptera. The eggs are numerous, one female depositing fifty-two in a single day. They are pearly white in color, about twenty-five one-hundredths millimeter in length, and are characteristically sculptured. The egg is very faintly attached to the

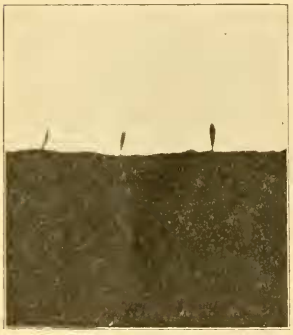

Fig. 2. Planidia of *Perilampus chrysopæ* var., attached to edge of oleander leaf and awaiting the approach of Chrysopa larva. (Original, photographed from life.)

Fig. 3. Planidium of Perilampusattached to egg-stalk of Chrysopa. (Original.)

[1] Determined by J. C. Crawford as *Perilampus chrysopæ* Crawford, new variety.

surface of the leaf at one end. Hatching takes place in seven to ten days and the first stage larva is of the planidium type described in the above mentioned paper. For several days previous to hatching the dark-colored planidium can be plainly discerned through the transparent egg-shell. The planidium is active immediately upon hatching, crawling rapidly about, but soon it attaches itself to the leaf by means of the caudal sucker and stands out at right angles to the surface. In this position it remains for days at a time, motionless, excepting when some insect comes within its reach, when it suddenly becomes frantically active, reaching and swaying back and forth in its attempt to attach itself to the prospective host. If the latter should unfortunately come too near, the planidium attaches itself with lightening-like quickness to a hair or bristle of the host. It then leisurely crawls down the hair to the host's body and attaches itself by its mouth-hooks. Quite often the planidia are found attached to the egg-stalk of *Chrysopa*, assuming a position at right angles to the axis of the stalk. This shows an interesting instinct in the planidium, since it may and actually does, as the writer has observed, waylay the young Chrysopa larva as it leaves the egg and crawls down the stalk. The prescience of the mother Chrysopa in placing her eggs at the end of a long egg-stalk to overcome the cannibalistic propensities of her progeny is in this case their undoing, since the planidium attached to the Chrysopa egg-stalk is sure to reach its proper host, while those upon the surface of a leaf are quite as likely to attach themselves to an aphid or other insect.[1]

The planidia are remarkably long-lived for such delicate creatures. I have had them live for a period of seventeen days without food of any kind and without changing their position. Those which are fortunate enough to become attached to a Chrysopa larva immediately, as mentioned above, crawl down the hair or bristle and by means of their mouthparts attach themselves to the skin of their host. Many of these planidia undoubtedly lose their opportunity to develop through the moulting of the Chrysopa larva, although sometimes, as observed by the writer in the laboratory, they succeed in changing their position from the

[1] In a note in the Journal of Economic Entomology, Vol. 9, p. 510, Mr. M. T. Smulyan mentions having found a Perilampus planidium on an aphid. Without doubt this is the young of a Chrysopa infesting species which attached itself to the wrong host. They will even grasp a camels hair brush if brought within their reach.

moult-skin to the newly moulted host. In cases where the Chrysopa larva died in the laboratory, the planidium invariably crawled out on the end of a hair, attached itself by the caudal sucker and awaited the approach of a new host. Apparently the planidium takes no nourishment until the Chrysopa larva spins its cocoon and pupates, after which it begins to feed and develops in much the same way as the writer has described for *P. hyalinus* (*loc. cit.*), excepting that it is never an internal parasite so far as has been observed.

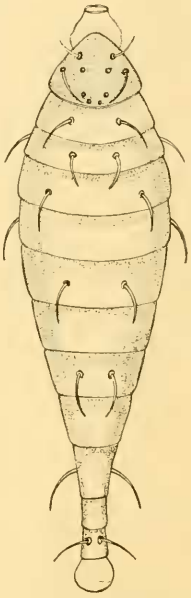

Fig. 4.—Planidium of *Perilampus chrysopæ* var., greatly enlarged. Dorsal view. (Original.)

It is difficult to understand just what is gained, from the standpoint of *Perilampus* infesting *Chrysopa*, by this extraordinary habit, since the Chrysopa larva is easily accessible to the normal method of oviposition and is in fact parasitized in the larval state by a number of parasites which oviposit directly into the host. In the case of *Perilampus hyalinus*, however, and other species having similar habits, the advantage is obvious, since by no other method could access be had to the larvæ of the primary parasites. In the case, too, of those species of Perilampus infesting wood-boring Coleoptera and gall-making and stem-infesting Lepidoptera (the correctness of which records the writer is frank to confess he previously looked upon with doubt), the usefulness of this method of oviposition taken with the active planidium stage is readily seen, since in this way access is easily gained to the endophagous host through the wanderings of the planidium. Needless to say, this type of reproduction forms one of the most extraordinary adaptations to environment in the entire field of entomology.